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Nest-Building and Spawning Behaviors in *Nocomis effusus* (Actinopterygii: Cyprinidae)

Eugene G. Maurakis[1,2] and **George E. Maurakis**[3]
[1]Science Museum of Virginia,
2500 West Broad Street, Richmond, VA 23220
[2]Biology Department, University of Richmond, VA 23173
[3]Bettie Weaver Elementary School, Midlothian, VA 23113

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ABSTRACT

Spawning behavior in *Nocomis effusus* is described from direct observations and review of videotapes made in Yellow Creek (Cumberland River drainage), Tennessee in 2003. Nest construction (i.e., excavating a concavity, forming a platform, and building a mound), and spawning behavior in *N. effusus* where a single breeding male excavates a pit and spawns with females on the upstream slope of his nest is like that described for *Nocomis asper* and *Nocomis biguttatus*. In digging a spawning pit, a male *N. effusus* reshapes and reorganizes substrate materials that results in spawning areas on the upstream slope of the nest composed of 6.0 and 11.3 mm size class pebbles. Aggressive behaviors (in order of increasing aggression) observed between nest-building and intruder male *N. effusus* were non-contact head displacement, non-contact body displacement, chase, circle swim, and head/body butt. Nest associates (i.e., species that congregate and may spawn in a nest but do not contribute to its construction) observed over nests of *N. effusus* were *Luxilus chrysocephalus* and *Lythrurus fasciolaris*.

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INTRODUCTION

Nocomis effusus, present in the Barren, Cumberland, Green, and Tennessee rivers in Kentucky and Tennessee (Etnier and Starnes, 1993), is one of seven species of *Nocomis* in all of which males use their jaws to construct gravel nests for spawning in spring (Lachner and Jenkins, 1971). The only investigation of breeding activities of *N. effusus* is an unpublished masters thesis by Henry (1999), who studied the reproductive ecology of the species in Little South Fork of the Cumberland River in Kentucky. Spawning behavior has been published for populations of close relatives, *Nocomis asper* by Maurakis and Roston (1998) and *Nocomis biguttatus*, by Vives (1990) and Maurakis et al. (1991). This paper describes spawning nests and behaviors in *N. effusus* and compares them to those in Henry (1999), and to those of the other two species (*N. asper* and *N. biguttatus*) in the *Nocomis biguttatus* species-group proposed by Lachner and Jenkins (1971) and Maurakis et al. (1991).

MATERIALS AND METHODS

Observations and videorecordings of fishes, and collections of nest and substrate data at nests of *N. effusus* were made at three localities in Yellow Creek (Cumberland drainage, Dickson Co. TN) on 14-15 June 2003: EGM-TN-575 (36° 12.434'N, 087° 31.714'W) at confluence with Cedar Creek, 4.8 km SE of Jct. TN 46 and TN 49 (two active nests; water temp.=19.2 C); EGM-TN-576 (36° 10.934'N, 087° 31.197'W), bridge on Maysville Rd., 75 m from TN 46, ~7.2 km SE of Jct. TN 46 and TN 49 (3 active nests; water temp.=19.1 C); and EGM-TN-577 (36° 07.465'N, 087° 29.481'W), bridge on Bishop Slab Rd. off TN 46, ~ 11.2 km NW of Dickson, TN (one active nest; water temp.=18.9 C). Nest dimensions and composition of nests (no. of nests) of *N. biguttatus* were made by Mark H. Sabaj (MHJ) at the following localities: Wisconsin: upper Mississippi River, Portage Co., MHS-WI-001 (1), Tomorrow River, WI St. Rt. 10 S of Amherst at Jct. Co. Rt. A, 24 June 1989. MHS-WI-003 (1), Plover River at Jct. Co. Rts. Y and K, 25 June 1989. MHS-WI-004 (1), Tomorrow River, 0.4 km off WI St. Rt. 10 near Jct. River Rd. 26 June 1989. MHS-WI-005 (1), Tomorrow River, 0.4 km off WI St. Rt. 10 near Jct. with River Rd., 26 August 1989. MHS-WI-006 (2), Tomorrow River, St. Rt. 10 bridge just S of Jct. Co. Rt. A, 26 August 1989. MHS-WI-007 (1), Tomorrow River, wayside off WI St. Rt. 10 N of bridge, 26 August 1989.

Videorecordings were made with a Canon DM-XL1A digital camera/recorder, equipped with a 16x zoom lens. Four hours of activities of fishes recorded on tape were reviewed at normal speed, in slow motion, and frame-by-frame to identify specific behaviors of female and male *N. effusus* following methods in Maurakis and Woolcott (1995). Six chronological categories reflecting the sequence of male-female interactions characteristic of a successful spawn, following Sabaj (1992) and Maurakis and Woolcott (1993), were used to resolve reproductive activities of male and female *N. effusus*: *interim* (behavior of male between spawns), *approach* (behavior of female directed towards interim male), *alignment* (behavior affecting orientation of a spawning pair over substrate), *run* (initiated by a female, synchronized movement of aligned pair over substrate), *clasp* (spawning act, i.e., momentary flexure of male's body about that of female at end of her *run*), and *dissociation* (behaviors of male and female affecting their separation immediately following the clasp). Behaviors other than those associated with the spawning sequence were considered disruptive of successful spawns.

A satellite male is one that deceptively mimics females and pairs simultaneously with true females and parental males (Gross, 1984). Nest associates are species that congregate and may spawn over a nest but do not contribute to its construction.

Stream width, depth, and water temperature; nest length, width, and height; and spawning pit diameter and depth were measured at each nest. Pebble samples were collected from upstream and downstream portions of nests with a 1 liter plastic beaker. Substrate samples, collected with the same device, were taken at random as far as 10 m from nests. Nest and substrate samples, stored in tagged plastic bags, were returned to the laboratory where each sample was air-dried and sifted through five custom-built wire sieves. Mesh sizes, restricted to commercially available prefabricated screen sizes, were 23.0 mm, 11.3 mm, 6.0 mm, 2.5 mm, and 0.8 mm. Material that sifted through the smallest size mesh (<0.8) was collected in a pan. Weight of material in each sieve or pan was used to calculate percentage of material per mesh size. Hereafter, all references to percentage of mesh size classes are based on weights. An electivity index (Ivlev, 1961) was calculated for each pebble size class per nest. The equation $E=(n-p)/(n+p)$ where E=pebble size selection, n=percentage of a particular pebble size in the nest, and p=the percentage of a particular pebble size in the substrate of the stream) was used to determine if selection of pebble size from the substrate was random. The electivity index was also used to determine if selection of pebble size in spawning areas was random relative to non-spawning areas of nests. Percentages and electivity values were transformed to arcsin equivalents prior to statistical analyses. ANOVA

TABLE 1. Mean (standard deviation; minimum-maximum) stream and active nest characteristics in *Nocomis effusus* collected from Yellow Creek, Dickson Co., TN, 14-15 June 2003; and *N. biguttatus* collected from Tomorrow and Plover rivers, Portage Co., WI, 24-26 June 1989 by Sabaj (see Materials and Methods).

	N. effusus		*N. biguttatus*	
Stream				
Spawning temp. (C)	19.1	(18.9-19.2)	21	(19-23)
Depth (cm)	70	(40-100)	39.8	(32.5-47)
Width (cm)	10.8	(3.5-18)	24.5	(9-40)
Nest				
Width (cm)	78.80	(51-118)	68	(54-82)
Length (cm)	88.40	(72-116)	64.5	(59-70)
Height (cm)	18.00	(14-24)	12.5	(12-13)
Pit diameter (cm)	5.00	(3.5-6.5)	10.00	(10)
Pit depth (cm)	3.24	(2.5-4)	4.00	(4)

and Duncan's Multiple range test (SAS, 2002) were used to compare average values of stream depth, substrate composition, nest composition, electivity of pebble sizes in each species, and spawning versus non-spawning substrates in nests of *N. effusus*.

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RESULTS

Nest building and spawning behaviors in *N. effusus* were observed at water temperatures ranging from 18.9-19.2 C in June, 2003. Water depth and stream width at nests averaged 0.7 (range=0.4-1.0 m) and 10.8 m (range=3.5-18.0 m), respectively (Table 1).

Nest Construction

A nest was constructed and guarded by a single male. Nest construction began when a male excavated with his jaws a concavity (~0.3 m in diameter) in the stream bed where he frequently aligned himself (head upstream). Excavated stones were moved to lateral margins of the concavity parallel to the water current. Then the male transported stones from lateral margins of the concavity and nearby stream substrates to cover the concavity. This resulted in a relatively flat platform of stones, elevated about 5 cm above the stream substrate, with a central flow-through trough. The upstream portion of the platform had fewer pebbles than posterior and lateral margins, thus resulting in a upstream tilt. A male periodically fanned the central flow-through trough with his anal fin. After forming the platform, a male collected pebbles as far as 15 m from the nest, and placed them onto the platform, eventually to form a conical mound nest. During the early stage of mound-building, the developing mound sometimes appeared somewhat as a donut as fewer stones were deposited in the center and upstream portion of the nest. When the mound was about halfway completed, the male deposited stones at the central apex of the nest more frequently, and then moved to the center of the upstream slope of the nest where he momentarily stopped before swimming away to collect other stones from the streambed. During the end of mound building, the male began to fan the center of the upstream slope of the nest with his

TABLE 2. Average percentages of nest material and substrate material around spawning nests of *Nocomis effusus* and *Nocomis biguttatus*. Underscored means do not differ significantly.

N. effusus	Nest material size class (mm)					
	0.8	<0.8	2.5	6.0	11.3	23.0
Mean%	0.1	0.1	0.2	3.8	41.9	53.9
F=66.67						
p<0.0001						
df =5						

N. biguttatus						
	0.8	<0.8	23.0	2.5	6.0	11.3
Mean%	0.2	0.7	*1.0*	*1.7*	38.0	58.4
F=92.9						
P<0.0001						
df =5						

N. effusus	Substrate material size class (mm)					
	<0.8	0.8	2.5	6.0	11.3	23.0
Mean%	0.1	0.1	3.55	11.4	13.4	71.6
F=672.64						
p<0.0001						
df=5						

N. biguttatus						
	0.8	2.5	<0.8	6.0	11.3	23.0
Mean%	1.2	2.9	3.9	10.6	23.9	57.5
F=22 .8						
p<0.0001						
df =5						

anal fin. Concentrating on this area, he began to reshape the upstream portion of the nest where he dug a pit, spending more time digging and fanning the pit, and moving larger stones away from the pit area. After spawning in a pit, a male covered it with gravel collected from the upstream slope of the nest, or occasionally from surrounding stream substrates, before excavating another spawning pit on the upstream portion of the nest.

In *N. effusus*, nest width, length, and height averaged 78.8, 88.4, and 18 cm, respectively; spawning pit depth and diameter averaged 3.2 and 5.0 cm, respectively (Table 1). In *N. biguttatus*, nest width, length, and height averaged 68, 64.5, and 12.5 cm, respectively; spawning pit depth and diameter averaged 4.0 and 10.0 cm, respectively (Table 1). Stream substrates where nests were constructed by each species were dominated by the 23 mm stone size class (Table 2).

In nests of *N. effusus*, average percent (41.9-53.9) of the 23.0 and 11.3 mm size class pebbles was significantly higher than those of other size classes (Table 3). In *N. biguttatus*, average percent (38-58.4) of the 11.3 and 6.0 mm size class pebbles were significantly higher than those of other size classes (Table 2). Average electivity value

TABLE 3. Average electivity value per size class in spawning nests of *Nocomis effusus* and *Nocomis biguttatus*. Underscored means do not differ significantly.

Nocomis effusus	Electivity per pebble size class (mm)					
	2.5	6.0	23.0	<0.8	0.8	11.3
Mean%	0.90	-0.54	-0.15	-0.07	-0.07	0.50
F=40.80						
P<0.0001						
df =5						
Nocomis biguttalus						
	23.0		0.8	2.5	11.3	6.0
Mean%	-0.88	-0.55	-0.52	-0.03	0.38	0.46
F=8.6						
P<0.0001						
df =5						

TABLE 4. Average percentages of spawning and non-spawning nest material in spawning nests of *Nocornis effusus*. Underscored means do not differ significantly.

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	Spawning substrate size class (mm)					
	0.8		2.5	6.0	23.0	11.3
Mean%	0.12	0.14	0.42	9.90	16.50	72.70
F=41 .60						
P<0.0001						
df =5						
	Non-spawning substrate size class (mm)					
	<0.8	0.8	2.5	6.0	11.3	23.0
Mean%	0.10	0.10	0.10	0.62	24.60	74.50
F=54.0						
P<0.0001						
df =5						

(0.50) for the 11.3 mm size class in nests of *N. effusus* was significantly greater than for other size classes (Table 3). In nests of *N. biguttatus*, average electivity values (0.38-0.46) for the 6.0 and 11.3 mm size class were significantly greater than for other size classes (Table 3).

Average percent (72.7) of the 11.3 mm size class of stones in spawning areas of nests of *N. effusus* was significantly greater than those (0.12-16.5) of other size classes (Table 4). At non-spawning substrates in nests of *N. effusus*, average percents (24.6-74.5) of the 11.3 and 23.0 mm size class stones were significantly greater than those (0.1-0.6) of other size classes (Table 4). Average electivity values (0.51-0.76) for the 11.3 and 6.0 mm size classes of stones in spawning areas of nests of *N. effusus* were

TABLE 5. Average electivity value per size class of stones in spawning substrates in nests of *Nocomis etjitsus*. Underscored means do not differ significantly.

	Spawning substrate class size (mm)					
	23.0	<0.8	0.8	2.5	11.3	6.0
Mean%	-0.68	0.13	0.13	0.34	0.51	0.76
F=1 8.78						
P<0.0001						
df =5						

significantly greater than those (-0.68-0.38) of the 23.0, 0.8, and <0.8 mm size class stones (Table 5).

Aggressive behaviors (in order of increasing aggression) observed between nest-building and intruder males were non-contact head displacement, non-contact body displacement, chase, circle swim, and head/body butt. No satellite male *N. effusus* were observed over nests.

Nest associate species of *N. effusus* were *Luxilus chrysocephalus* and *Lythrurus fasciolaris*. On two occasions, a male *L. chrysocephalus* periodically moved into and out of the central flow-through trough during platform construction by a male *N. effusus*. *Lythrurus fasciolaris* periodically maintained a position over the upstream slope of a nest regardless of the presence of the nest-building male *N. effusus*. Nest associates did not congregate over the nest until after a nest-building male *N. effusus* increased the frequency of fanning the upstream slope of the nest and later the spawning pit with his anal fin.

Spawning analysis:

Interim: An interim male *N. effusus* engaged in typical *Nocomis* nest-building (i.e., excavating a concavity, forming a platform, and constructing a mound); and pit digging, pit fanning, and pit posturing interim behaviors like those described for breeding male *N. asper* and *N. biguttatus* by Maurakis and Roston (1998) and Maurakis et al. (1991), and those in *N. leptocephalus* (Sabaj, 1992).

Approach: Female *N. effusus*, hovering over the rear or lateral margins of a nest, approached the spawning pit singly from downstream regardless of the presence of the nest-building male. A successful approach occurred when a female moved into a spawning pit and beneath the postured male. Frequently, a female immediately returned to the pit after dissociation.

Alignment: After the approach, a female aligned parallel to the water current, pressed her belly to the substrate of the pit, and either immediately began her run, or momentarily remained in this position. In response, the male tilted his body toward the female.

Run: The run (about 2-3 cm), initiated by a female, began when she quivered her tail and moved slightly upstream. The male responded with rapid tail beats and moved forward with the female. With her body pressed to the spawning pit, the female moved forward to the upstream slope of the pit, gaped, and retroflexed (i.e., the immediate pitching of her head vertically while rolling the anterior portion of her body away from the male, movements that put her dorsum in contact with the male's anterior flank).

Females often made a run with retroflexure in the pit when a breeding male *N. effusus* was not present.

Clasp: As in *N. asper* and *N. biguttatus*, a male *N. effusus* initiated his clasp as his mate retroflexed. He turned his head toward the female, curved his posterior flank over her back and drove it into her side between her pectoral and pelvic girdles. As the male's body (from head to caudal fin) contracted into a semicircle during the clasp (lasting up to one second), his urogenital pore was pressed to the dorsolateral surface of the female's caudal peduncle, as her urogenital pore remained in contact with the substrate on the upstream rim of the pit.

Dissociation: When the male's body relaxed after contraction, the spawning pair dissociated. The male usually drifted downstream and resumed interim behavior while the female continued to rise vertically into the water column, then regained horizontal equilibrium, and either moved to the downstream portion of the nest or drifted just downstream of the male and initiated another approach.

DISCUSSION

Nocomis effusus was observed spawning at water temperatures ranging from 18.9-19.2 C in June, comparable to water temperatures (19-21 C) at peak spawning between the last week of May through the second week of June reported by Henry (1999) for the species in Kentucky. Nest-building and spawning in *N. effusus* probably occurs over several weeks in Tennessee, much like that reported for the species by Henry (1999) and for a closely related species, *N. biguttatus,* which spawns (water temperature range=16-26 C) from May through early July, but predominately during a three-four week period from mid-May to mid-June (Vives, 1990). Sabaj (pers. comm.) observed spawning in *N. biguttatus* between 19-23 C in Wisconsin in late June, 1989.

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Our average nest width (78.8 cm), length (88.4 cm), and height (18 cm) for *N. effusus* compare well to those (71, 81, and 13.5 cm, respectively) reported by Henry (1999) for the species, and to those (68, 64.5 and 12.5 cm, respectively) of nests of *N. biguttatus* (Table 1). Henry (1999), who used the substrate particle diameter classification system in Cowardin et al. (1979) did not present percent composition of various size classes of stones in nests or substrates around nests of *N. effusus* in his study. He reported stone sizes in nests of *N. effusus* ranging from 26.4-41.8 mm, retained by our 23.0 mm size class, and 18.9-21.1 mm, held by our 11.3 mm size class. Our custom-made sieves (i.e., sizes=23.0, 11.3, 6.0, 2.5, 0.8, and <0.8 mm) and use of an electivity index present a more precise account of composition of substrate materials in nests, particularly in identifying the particular size classes (11.3 and 6.0 mm) where spawning occurred in pits on the upstream slope of nests of *N. effusus* as well as those in *N. biguttatus* (Tables 2-3). Maurakis and Zorman (2001) stated there was a preference for 6.0 and 11.3 mm size class pebbles and significant selections against larger (23.0 mm) and smaller (2.5, 0.8, and <0.8 mm) size classes of pebbles in spawning areas in nests of *Nocomis micropogon*, *Nocomis platyrhynchus*, *Nocomis raneyi*, and *Nocomis leptocephalus*. We concur with Maurakis and Zorman (2001) that in reshaping and reorganizing the spawning substrate, a male *Nocomis* removes obstructions (e.g. stones >11.3 mm size class) that may interfere with the sequence of spawning behaviors. Secondly, size uniformity (≥6.0, ≥11.3 mm) of pebbles and resultant interstices in spawning substrates of *Nocomis* nests afford conditions that prevent crushing and smothering of buried eggs and post-hatch larvae (Maurakis and Zorman, 2001). Egg diameter in *N. effusus* averaged 2.89 mm (range=2.38-3.44)(Henry, 1999), comparable to those (2.0-2.8 mm) reported by Maurakis and Zorman (2001) for *N. micropogon*, *N. platyrhynchus*, *N. raneyi*, and *N. leptocephalus*, who related spawning substrate material size (i.e., 6-11.3 mm) to egg diameter.

The sequence of male-female interactions characteristic of a successful spawn in *N. effusus* is like that described for the species by Henry (1999); for *N. asper* by Maurakis and Roston (1998); and for *N. biguttatus* by Vives (1990) and Maurakis et al. (1991). There are no apparent differences in male breeding behaviors (excavating a concavity, forming a platform, and constructing a mound; pit digging, pit fanning, and pit posturing) among *N. effusus*, *N. asper* (Maurakis and Roston, 1998), *N. biguttatus* (Vives, 1990; Maurakis et al., 1991), and *N. leptocephalus* (Sabaj, 1992 and Sabaj et al. 2000). However, the behavior of a single male constructing and defending one nest in each of *N. effusus*, *N. asper* and *N. biguttatus* is like that in *N. micropogon*, *N. platyrhynchus*, and *N. raneyi* (Maurakis et al., 1991; Maurakis, 1999; Sabaj et al., 2000) but unlike that in *N. leptocephalus* where several males may excavate their own spawning pits alongside that of the nest-building male, after sequentially establishing territories on the upstream slope of the nest (Maurakis et al., 1990; Maurakis et al., 1997; Sabaj et al., 2000).

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